IOCRINUS IN THE ORDOVICIAN OF ENGLAND AND WALES

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ABSTRACT. *Iocrinus* contains more described species than any other crinoid genus known from the Ordovician of England and Wales. British species of this taxon generally have a smooth, conical, dorsal cup and a proximal stem which is pentagonal in transverse section. A new species, *I. pauli*, from the Llanvirn of the Builth Wells area, is unusual in having a ribbed dorsal cup and a proxistele of pentastellate transverse section. These features have hitherto been noted only in *Iocrinus* from North America. *Iocrinus* sp. cf. *I. pauli* is recognized from the Lower Llandeilo of Dyfed on the basis of disarticulated columnals and a poorly preserved crown. *I. whitteryi* Ramsbottom, from the Caradoc of Shropshire, is refigured to illustrate such diagnostic features as the anal sac, the brachial articulum, and the stem. The family Iocrinidae Moore and Laudon is now known to include six genera. With one exception of Lower Llandovery age, all known iocrinids are of Ordovician age, and can be divided into two groups depending upon the complexity of the anal series.

THE disparid crinoid genus *Iocrinus* Hall is known from the Ordovician of North America and the United Kingdom. The first British species were not recognized until 1961, when Ramsbottom described *I. shelvensis* and *I. whitteryi*. He also tentatively suggested that *Dendrocrinus cambriensis* Hicks may be an *Iocrinus*. Bates (1965) described a further species, *I. brithdirensis*, and later (1968) showed that *D. cambriensis* was not an *Iocrinus*, but a member of a new disparid genus *Ramseyocrinus*.

Iocrinus is the most diverse crinoid genus found in the British Ordovician south of the Iapetus Suture. Hitherto, British species have been differentiated from those of North America in having a smooth, conical, dorsal cup that lacks ribbing and a proximal stem that is pentagonal, rather than pentastellate, in transverse section. A new species from the mid-Ordovician of Wales, described below, shows those features which hitherto were thought to be limited to North American species of *Iocrinus*.

Of the other British species of *Iocrinus*, *I. shelvensis* (Ramsbottom 1961, pp. 3–4, pl. 1, figs. 3–8; Donovan 1986, p. 27, pl. 1, figs. 3, 4, 8, 9, text-fig. 12A–J) and *I. brithdirensis* (Bates 1965; Donovan 1986, p. 25, text-fig. 12K) are both adequately described elsewhere. However, Ramsbottom's original illustration of *I. whitteryi* (1961, pl. 1, fig. 9) did not show the diagnostic features of the genus such as the anal sac. This species is reillustrated below.

Crinoid terminology used herein follows Moore *et al.* (1968), Ubaghs (1978), and Webster (1974). The synonymy of *I. whitteryi* was compiled in the style advocated by Matthews (1973).

SYSTEMATIC PALAEONTOLOGY

Class CRINOIDEA J. S. Miller, 1821
Order DISPARIDA Moore and Laudon, 1943
Family IOCRINIDAE Moore and Laudon, 1943
Genus IOCRINUS Hall, 1866

Type species. By monotypy; *Heterocrinus* (*Iocrinus*) *polyxo* Hall 1866 (= *Heterocrinus subcrassus* Meek and Worthen 1865).

Other species. *I. brithdirensis* Bates 1965; *I. crassus* (Meek and Worthen 1865); *I. pauli* sp. nov.; *I. shelvensis* Ramsbottom 1961; *I. similis* (E. Billings 1857); *I. trentonensis* Walcott 1883; *I. whitteryi* Ramsbottom 1961.

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Diagnosis. (Modified after Moore *et al.* 1978, p. T552; Kelly 1978, p. 54.) Dorsal cup conical to slightly bowl-shaped, composed of five prominent basal plates and five larger radial ossicles. An anibrachial, supported by the C ray radial, in turn supports the anal series on the left side and a free arm on the right. Anal sac complex. Arms with at least four isotomous branches. Column transversely pentagonal or pentastellate proximally, pentagonal in the mesistele and circular distally. Permanent attachment by distal, non-planar, spiral coil.

Remarks. We agree with Ubaghs (1978, p. T118) that the plate supported by the radial in the C ray is an anibrachial, rather than a superradial (Moore *et al.* 1978, p. T552).

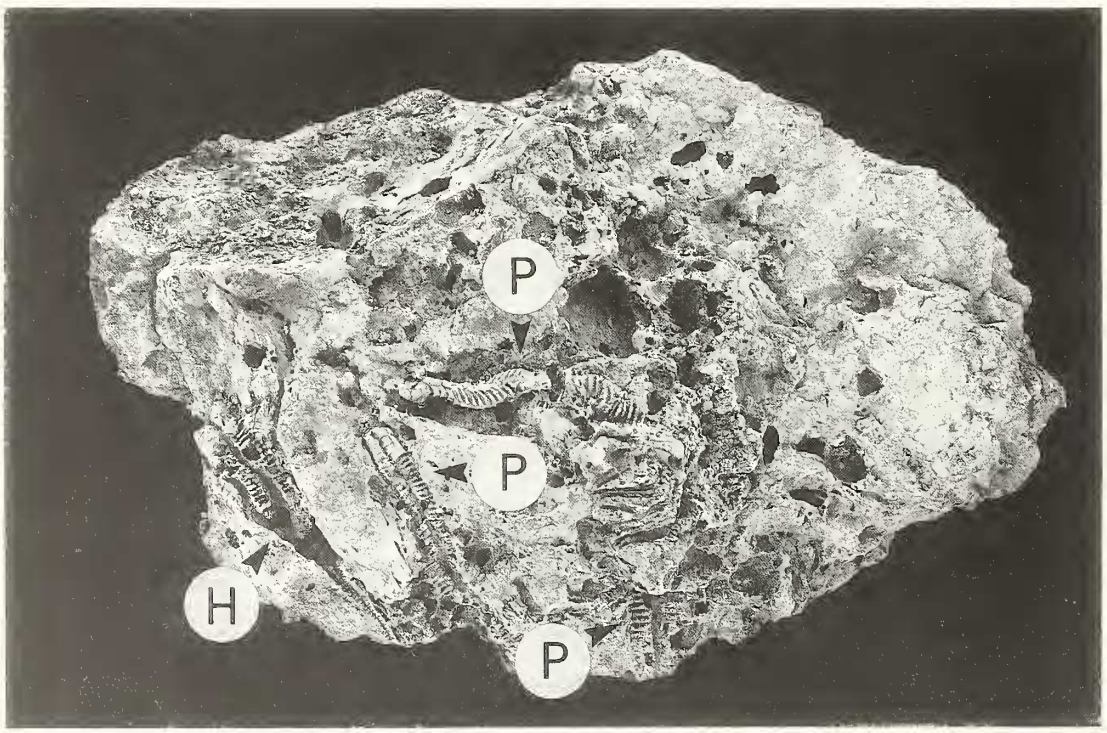
Iocrinus pauli sp. nov.

Text-figs. 1–3

Derivation of name. For Dr Christopher R. C. Paul.

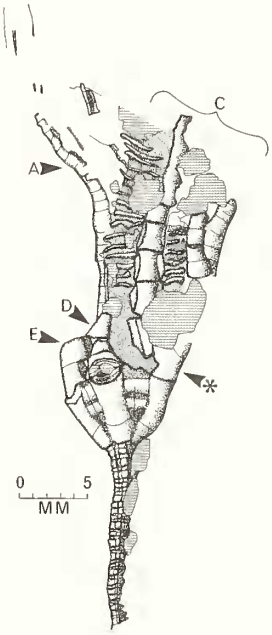
Type material. The holotype and three paratype anal sacs occur together on a single slab, British Museum (Natural History) (BMNH) E71413 (text-figs. 1 and 2). An external mould without counterpart. Probably from near Hundred House (see below).

Other material and locality. A single, well-preserved specimen in the private collection of Mr J. J. Savill (text-fig. 3). An external mould without counterpart. From National Grid Reference SO 0970 5590 (Mr C. Moore, written comm.), on the road from Hundred House to Llandrindod Wells, Powys, mid-Wales. *Didymograptus bifidus* Beds, although there is some doubt as to the precise age of this locality (see below). A cast is deposited in the BMNH E71424.



TEXT-FIG. 1. *Iocrinus pauli* sp. nov., type specimens, BMNH E71413. All specimens preserved as external moulds, apart from some portions of anal sac which appear to have been infilled. Holotype (H) and paratypes (P) indicated. × 1.

Horizon. The fauna associated with the type material suggests that this species may be either late Lower Llanvirn or early Upper Llanvirn. A dissociated trilobite pygidium has been identified as *Flexicalymene* sp. cf. *F. aurora* Hughes (BMNH It 19109) by Drs R. A. Fortey and S. F. Morris. Common brachiopods (BMNH Bc 10656) are assigned to *Tissintia plana* (Williams) (Dr D. A. T. Harper, written comm.). Thomas *et al.* (1984, fig. 10) suggested that *F. aurora* ranges from the Lower into the earliest Upper Llanvirn, although Hughes (1969, p. 82) considered the species to be limited to the uppermost Lower Llanvirn. Lockley and Williams (1981, table, p. 5) noted that *T. plana* occurs in the Upper Llanvirn and Lower Llandeilo of the Llandeilo area.



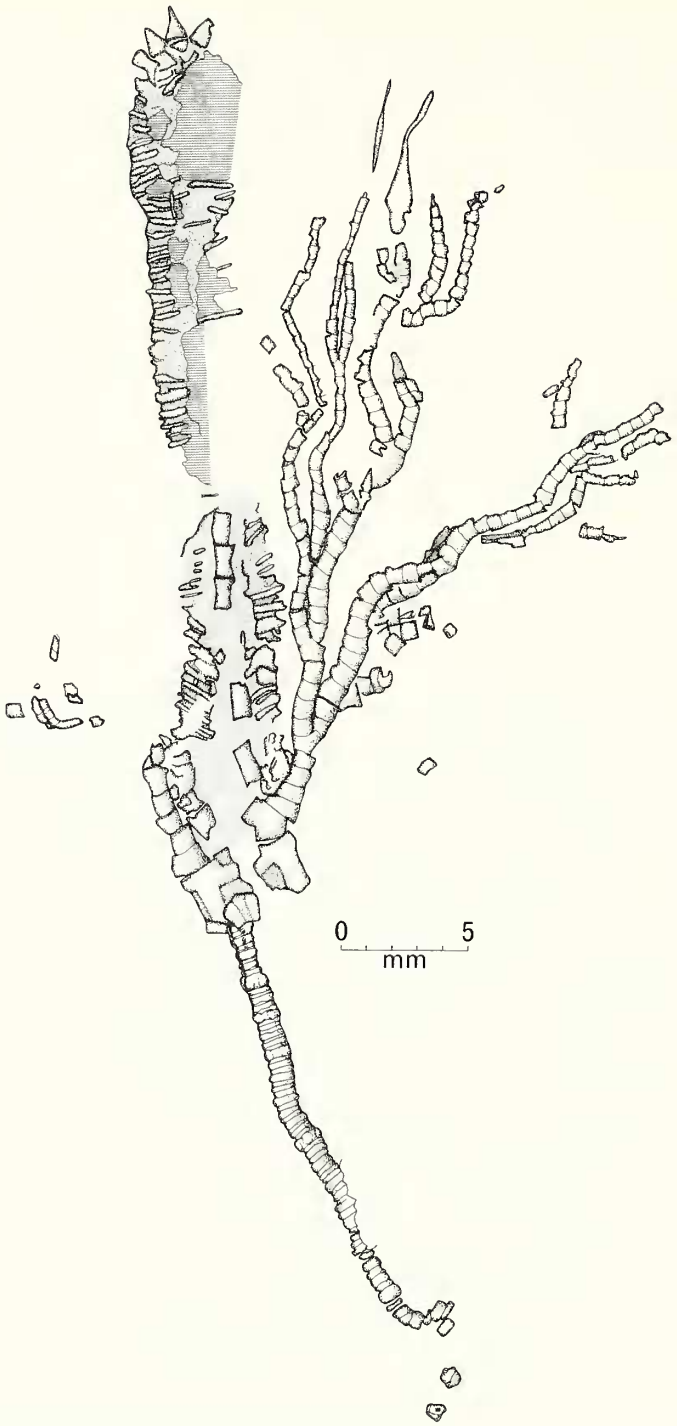
TEXT-FIG. 2. *Iocrinus pauli* sp. nov. holotype, BMNH E71413. Camera lucida drawing from a latex cast. A, C, D, and E rays indicated. * = anibrachial plate.

Diagnosis. A species of *Iocrinus* with a proxistele of pentastellate section and a ribbed, conical dorsal cup. Basals about as high as wide, radial plates higher than wide. Five primibrachials per arm, with at least five secundibrachials, five to nine(?) tertibrachials and about thirteen quartibrachials per branch.

Description. Form of attachment uncertain, but the dististele of the BMNH E71424 (text-fig. 3) is curved through about 90° (although slightly disarticulated), so that it is reminiscent of the distal stem in *I. brithdirensis* (cf. Bates 1965, pl. 45, fig. 5; Donovan 1986, text-fig. 12K). *I. pauli* was, therefore, probably attached by a distal, non-planar, spiral coil (Brett 1981), as were other species of *Iocrinus* (Kelly 1978).

The holotype retains the proximal 13·5 mm of stem (text-figs. 1 and 2) and the column of BMNH E71424 is over 20 mm long (text-fig. 3), but neither is complete. The column is pentastellate in transverse section proximally, changing to pentagonal shortly below the cup. Latera strongly convex, except in tertinternodals and quartinternodals, which have weakly convex to planar latera. Articular facet divided into five equal areola petals surrounding a central, pentagonal lumen. Articulation uncertain, either symplectial or synostosial. Column heteromorphic, N1(?) proximally to N434243414342434 distally (notation after Webster 1974). Nodals highest, quartinternodals lowest. Columnal angles swollen, except in quartinternodals.

Dorsal cup monocyclic, wider than high, with an angular, conical outline. Basals low, pentagonal, concave, presumably five in number, with longitudinal grooves corresponding to the folds of the proximal column. Radials as high as wide (about twice as high as basals), presumably five in number, with prominent, central, longitudinal ribs radially positioned and corresponding to the angles of the column. Regions between ribs



TEXT-FIG. 3. *Iocrinus pauli* sp. nov., BMNH E71424. Camera lucida drawing from a latex cast. C ray (and some dissociated brachials from the B ray?) occupies the upper right and centre of the figure. Note the slightly disarticulated anal pyramid.

depressed, but a further pair of ridges, parallel to the adoral surface of the cup, link the main ribs of adjacent radials. All radials observed are of equal size.

The complex anal sac arises from the anibrachial plate in the C ray and is about 30 mm long by 4 mm wide in BMNH E71424, reaching 35+ mm in the longest paratype (text-fig. 1). The proximal anal series is best seen in the holotype (text-fig. 2) where it comprises a series of elongate plates, slightly longer than wide, with central, convex latera flanked by planar flanges. The anal series supports lateral sac covering plates. The anal sac is terminated by an anal pyramid (text-fig. 3) composed of solid, conical ossicles.

The arms are uniserial, non-pinnulate, isotomously branching at least four times and presumably five in number. The C ray radial supports an anibrachial (text-figs. 2 and 3). Where apparent, there are five primibrachials per ray, including those above the anibrachial. Following each successive bifurcation, there are five secundibrachials, five to nine(?) tertibrachials, and about thirteen (minimum) quartibrachials per branch. Brachials are stout proximally, slender distally. Latera are planar and unsculptured. Adoral groove V-shaped, with brachials having a U-shaped section. Brachials are about as high as wide proximally, but higher than wide distally.

Remarks. I. pauli sp. nov. is easily distinguished from the other British species of *Iocrinus*, *I. brithdireusis* Bates, *I. shelvensis* Ramsbottom, and *I. whitteryi* Ramsbottom, all of which have smooth, conical, dorsal cups and, where known, a proxistele of pentagonal section. *I. pauli* most closely resembles the North American species *I. subcrassus* (Meek and Worthen). However, *I. subcrassus* has basals and radials that are wider than high, whereas in *I. pauli* basals are about as wide as high, while radials are slightly higher than wide. The base of the dorsal cup in *I. subcrassus* appears broader (cf. Moore 1962, pl. 2, figs. 1 and 2*a*; Kelly 1978, pl. 1, figs. 12 and 13), with a lower anibrachial plate (cf. Kelly 1978, text-fig. 5), than in *I. pauli*. Further, it may be relevant that *I. pauli* is significantly older than the first *I. subcrassus* (text-fig. 6) and no other crinoid species has yet been recognized from both sides of the Iapetus Ocean in the Ordovician.

Of the other species of *Iocrinus* from North America, *I. crassus* (Meek and Worthen) has an unusually large dorsal cup, with a radial : basal height ratio of about 3 : 2, compared with 2 : 1 in *I. pauli*. *I. similis* E. Billings is probably aberrant (Kelly 1978, p. 61) and is only known from a unique holotype. The proxistele is pentagonal and an additional ossicle is present between the C ray radial and the anibrachial. *I. trentonensis* Walcott is very similar to *I. subcrassus*. A new species of *Iocrinus* from the lower Ordovician of North America is awaiting description by Kelly.

Iocrinus sp. cf. *I. pauli* sp. nov.

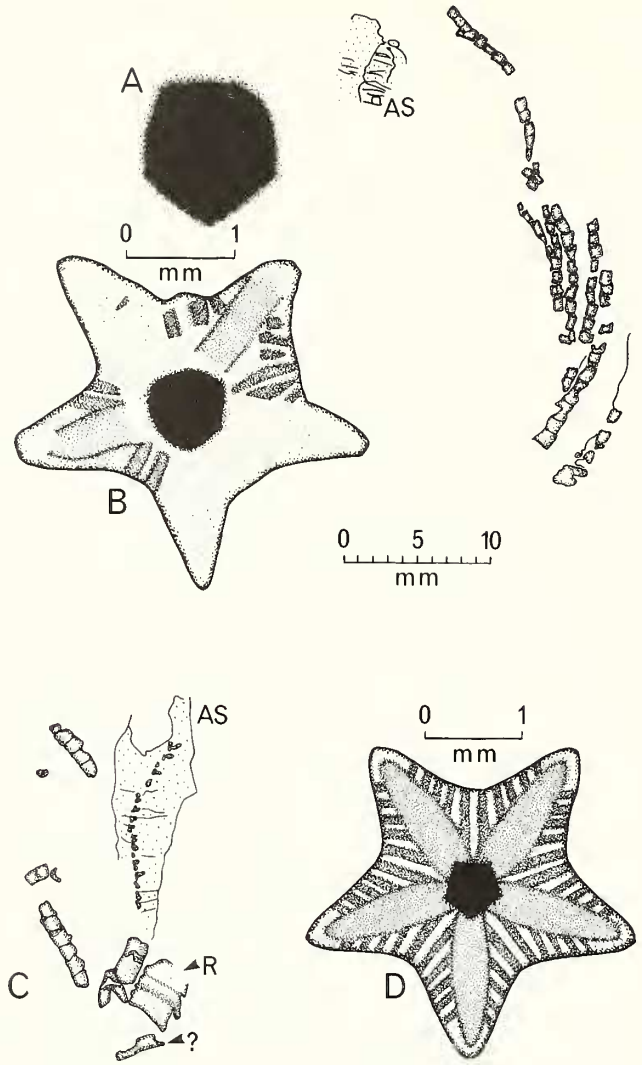
Text-fig. 4

Material, locality, and horizon. A partially disarticulated crown, BMNH E69597, an external mould without counterpart, plus a brachial, BMNH E71418, and five columnals, BMNH E71414–E71416, E71417*a*, *b* (counterparts), E71419*a–c* (counterparts), all of which are external moulds. All from the Lower Llandeilo, Llandeilo Flags, Ffairfach, Dyfed, South Wales, NGR SN 628 212 (Bassett 1982, p. 284, fig. 3).

Description. Disarticulated, pentastellate to pentagonal columnals with a small, central, pentagonal lumen (text-fig. 4A, B, D). Lumen angles correspond to the angles of the columnal. Five separate areola petals, which vary from rounded-pentagonal to elongate-triangular in outline, correspond to the angles of the lumen. Symplectial articulation, with parallel crenulae extending between areola petals in more stellate columnals (text-fig. 4B, D). No pentastellate columnal preserves a crenularium at the extremities of the rays. Columnals low, with slightly convex latera.

Dorsal cup unknown apart from a single, disarticulated, ?radial plate (text-fig. 4C). The anal sac is incomplete, but the proximal 17 mm is preserved, along with a more distal fragment. Two parallel series of lateral sac covering plates are apparent, with a suture between them that possibly conceals the pseudo-anal series (cf. Kelly 1978, text-fig. 4E).

Arms long, apparently at least 75 mm minimum (text-fig. 4C), uniserial, non-pinnulate, and branching isotomously. The number of branching events is unknown, but one or ?two are apparent distally. Proximal brachials are about as high as wide. Distal brachials are smaller and higher than wide. Brachials have a U-shaped section with a deep, broad, V-shaped adoral groove. Depressed, crescentic ligament pit aboral to the adoral groove.



TEXT-FIG. 4. *Iocrinus* sp. cf. *I. pauli* sp. nov. A, BMNH E71417*b*, lumen. B, BMNH E71415, articular facet. C, BMNH E69597, partially disarticulated crown. AS = anal sac; R = radial; ? = plate of uncertain affinity; other structures are fragments of arms or disarticulated brachials. D, restoration of articular facet. Apart from D, all figures are camera lucida drawings from external moulds (A, B) or a latex cast (C).

Remarks. Features such as the pattern of arm branching, the brachial facet architecture, the large anal sac, the outline of columnals, and the sculpture of their facets, all indicate that this species is a typical *Iocrinus*. It is tentatively recognized as an *Iocrinus* similar to *I. pauli*, the only British species with a pentastellate proxistele and ribbed radials. However, the Ffairfach species differs from the available material of *I. pauli* in having a larger crown.

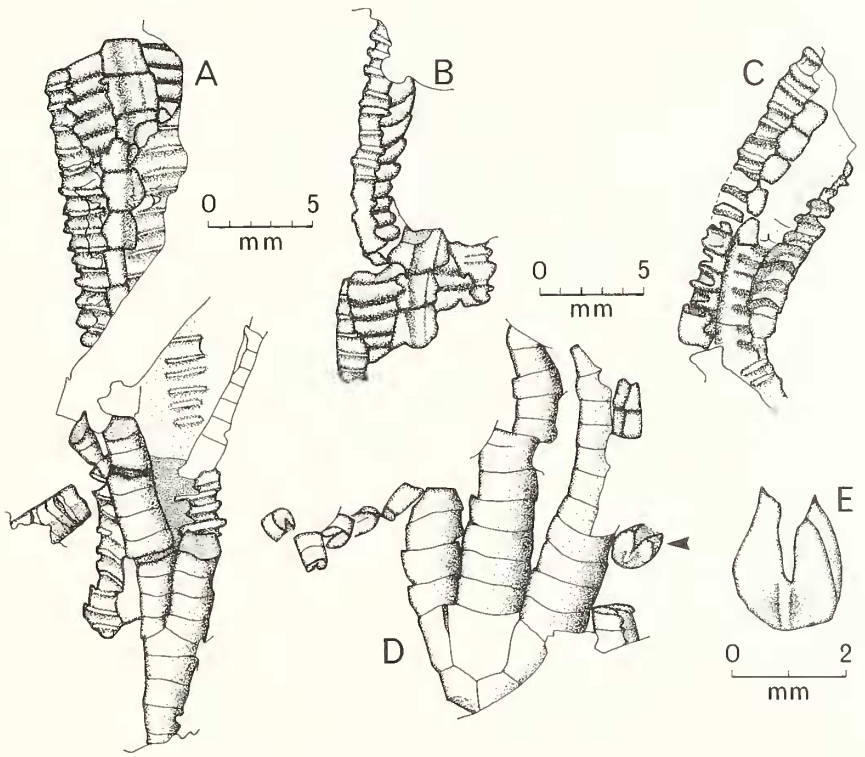
Iocrinus whitteryi Ramsbottom, 1961

Text-fig. 5

1869 *Cyathocrinus* sp.; Morton, p. 19.
v* 1961 *Iocrinus whitteryi* sp. nov., Ramsbottom, p. 5, pl. 1, fig. 9.
1973 *Iocrinus whitteryi* Ramsbottom; Webster, p. 157.
1978 *Iocrinus whitteryi* Ramsbottom; Kelly, pp. 63, 64.
1986 *Iocrinus whitteryi* Ramsbottom; Donovan, p. 21.

Material, locality, and horizon. Holotype, BMNH E49603, an external mould without counterpart. Paratypes, BMNH E1365, E49604, E49605 (all external moulds without counterparts); British Geological Survey (BGS GSM) 85720, 85720*a* (counterpart external moulds), 85721 (wax squeeze of holotype). All specimens are from Whittery Quarry, east of Marrington Dingle, near Chirbury, Shropshire, NGR SO 274 982. Chirbury Formation, Whittery Shale Member(?), Caradoc, Soudleyan (Whittard 1979, locality 299, p. 56, fig. 33).

Remarks. Ramsbottom (1961, p. 5) gave an adequate description of *I. whittery*, but the associated illustration (pl. 1, fig. 9) is undiagnostic of *Iocrinus*. Text-fig. 5 is therefore included herein to show those features of *I. whitteryi* that are typical of the genus.



TEXT-FIG. 5. *Iocrinus whitteryi* Ramsbottom, 1961. All paratypes apart from D, E. A, B, BMNH E49604. A pair of anal sacs, juxtaposed as preserved, and showing the morphology of both the internal and external surfaces. Both are in a similar orientation, with the plates of the anal series facing into the page. A short pluricolumnal is illustrated to the left of A, which is also associated with an arm fragment that branches twice. C, BMNH E1365. A further fragment of anal sac. D, E, BMNH E49603, holotype. D, dorsal cup showing three rays and some dissociated brachials. E, articular facet of brachial arrowed in D. All camera lucida drawings from latex casts. Not all fragments from each specimen have been illustrated.

The holotype, sadly lacking a counterpart, is the only known dorsal cup (text-fig. 5D; Ramsbottom 1961, pl. 1, fig. 9). This shows three rays, none of which includes an anibrachial and associated anal series. This specimen must therefore represent either the D–E–A or the E–A–B rays. None of the arms of the holotype appears to branch (but note branching at the ?primaxilliary and ?secundaxilliary levels in text-fig. 5A), so the primaxilliary must be at the level of $1Br_{12}$ or above. Dissociated brachial ossicles on the same slab, apparently derived from the holotype, show an articular facet architecture similar to that of *I. shelvensis* Ramsbottom (text-fig. 5E).

The anal sacs attributed to *I. whitteryi* (text-fig. 5A–C) are comparable to those known from other species of *Iocrinus* (cf. Ramsbottom 1961, pl. 1, fig. 6; Moore 1962, pl. 2, fig. 2*a–e*; Bates 1965, pl. 45, figs. 1, 2, 4–6; Kelly 1978, pp. 10–25, text-fig. 4, pl. 1, figs. 1–3, 5, 6, 14). This complex structure is diagnostic of the genus. Additionally, a short pluricolumnal, previously undetected, has been recognized on one of the paratype slabs of *I. whitteryi* (text-fig. 5A). This appears to be pentagonal in section, with rounded angles, and is heteromorphic. It is not dissimilar to some of the less nodose, pentagonal columns of other species of *Iocrinus*.

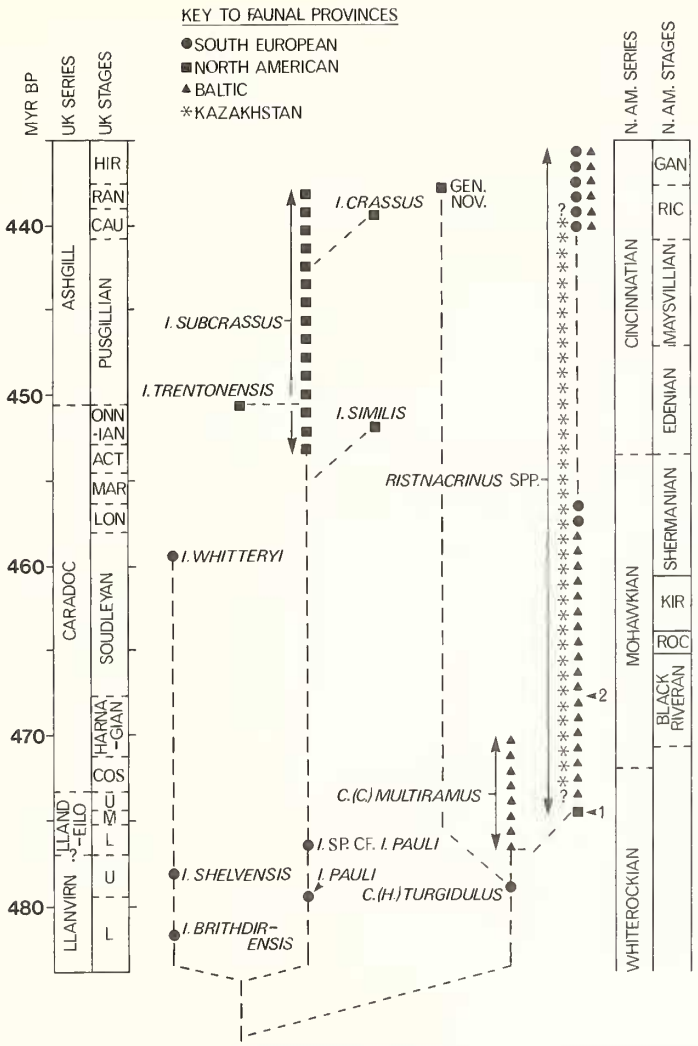
PHYLOGENY OF THE IOCRINIDAE

The disparid crinoid family Iocrinidae is now known to have contained at least six genera, spanning the interval lower Ordovician to Lower Llandovery (the only known Lower Ordovician species, *Iocrinus* sp. nov., is awaiting description by Kelly and is not included in this analysis). Iocrinid genera are differentiated on the basis of column structure, form of attachment, shape of the dorsal cup, basals exposed or cryptic, interbrachial plates present or absent, first primibrachials free or attached, and the structure of the anal series. On the basis of these characteristics, it is suggested that the iocrinids appear to be divided into two natural groups. These groups can easily be recognized, comprising those species which have either a complex (*Iocrinus*) or a simple (*Caleidocrinus* + *Ristnacrinus* + gen. nov.) anal series (text-fig. 6).

Iocrinus itself can be divided into two lineages, based on whether the proxistele is pentagonal or pentastellate in section and whether the dorsal cup is unsculptured or ribbed, respectively. Kelly (1978) considered that the ribbed species probably evolved from an ancestor with a smooth cup, but the occurrence of *I. pauli* suggests that the time of divergence of these two lineages was much earlier than he originally postulated. In text-fig. 6 the suggested relationships of the later species with a ribbed dorsal cup essentially follows Kelly (1978, text-fig. 15), while those for species with an unsculptured dorsal cup follows Donovan (1985*a*, fig. 8).

The features of the two species of *Caleidocrinus* Waagen and Jahn, and the relationship of *Caleidocrinus* to *Ristnacrinus* Öpik, have also been discussed in detail elsewhere (Donovan 1985*a*). *Ristnacrinus* is particularly well recorded on the basis of dissociated columnals, although at least some of these may be derived from *Caleidocrinus* (*C.*) *multiramus* Barrande. Only the type species of *Ristnacrinus*, *R. marinus* Öpik, is known from relatively complete material. ?*R. altobasalis* Brower and Veinus is poorly known and its generic assignment is, at best, dubious. It is perhaps significant that the distinctive columnals of *Ristnacrinus* have not been reported from North America. *R. cirrifer* Le Menn is based only upon cirriferous columnals. As some columnals of the type species are cirriferous and indistinguishable from Le Menn's species, this suggests that *R. cirrifer* is invalid. Four further species based on disarticulated columnals (Stukalina 1980) appear to be morphologically distinct. However, because of the general uncertainty regarding the subdivision of *Ristnacrinus*, this genus has been left undivided in text-fig. 6.

A new genus (Donovan, in press) differs from *Iocrinus* in lacking a large and complex anal sac. The basal plates of *Caleidocrinus* are either low or cryptic (Donovan 1985*a*) and interbrachial plates are present, whereas in the new genus basals are prominent and interbrachial plates are absent. *Ristnacrinus* has a slender dorsal cup with cryptic basals and a circlet of five radials supporting five fixed primibrachs (including the anibrachial in the C ray). The dorsal cup in the new genus is broad, tapering towards the base, and all brachials are free. The new genus is most similar to *Caleidocrinus* (*H.*) *turgidulus* Ramsbottom.



TEXT-FIG. 6. A probable phylogeny of the known iocrinids, showing the distribution of species in both time and space. Faunal data derived from Bates (1965), Briskeby (1981), Brower and Veinus (1974), Chauvel and Le Menn (1973), Chauvel *et al.* (1975), Donovan (1984, 1985*a*, *b*, 1986, in press), Kelly (1978), Öpik (1934), Ramsbottom (1961), and Stukalina (1980). Stratigraphic data principally from Ross *et al.* (1982), but also from Williams *et al.* (1972). Key: *I* = *Iocrinus*; *C* = *Caleidocrinus*; *H* = *Huxleyocrinus*; 1 = ?*Ristnacrinus altobasalis* Brower and Veinus; 2 = *Ristnacrinus marinus* Öpik.

The precise relationships of two further species of iocrinid are unknown and they are not included in text-fig. 6. Both belong to monospecific genera and both retain a pentameric column. This is presumably a primitive feature, yet one of these species, *Pariocrinus heterodactylus* Eckert, 1984, from the Lower Silurian of Ontario, is the youngest known iocrinid. This species has an elongate anal tube, rather than a sac as in *Iocrinus*, and arm branching above the primaxillary is heterotomous, rather than isotomous.

The second species with a pentameric column is *Peltacrinus sculptatus* Warn, 1982, from the Black Riveran, Bromide Formation of Oklahoma. This also supports a tube-like anal series. The dorsal cup is ribbed, with a flared base. Arm branching appears to be isotomous throughout.

The true diversity of the genus *Iocrinus* is probably underestimated in text-fig. 6. Numerous *Iocrinus*-like columnals have been recognized from the Middle and Upper Ordovician of Britain (Donovan 1983) and have been particularly well reported in the Russian literature. However, until more complete specimens are known, it would be premature to assign there dissociated plates to new species of *Iocrinus*.

Acknowledgements. We thank Mr Charles Buist, who found the original specimens of *I. pauli*, and Mr Jeremy J. Savill for supplying us with a cast of his specimen. Mr David N. Lewis (BMNH) kindly supplied casts of *I. whitteryi* and arranged for photography of BMNH E71413. Dr H. Ivimey-Cook (BGS) sent SKD the paratypes of *I. whitteryi*. We give special thanks to Drs R. A. Fortey, S. F. Morris (both BMNH), and D. A. T. Harper (University College, Galway) for identifying our trilobite and brachiopod material. Dr Peter R. Sheldon (Trinity College, Dublin) gave invaluable help in suggesting the probable stratigraphic position of *I. pauli*.

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